

## EARLY LINEAGES IN *APIALES*: INSIGHTS FROM MORPHOLOGY, WOOD ANATOMY AND MOLECULAR DATA

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Recent molecular studies indicate that the araliaceous tribes *Myodocarpeae* R. Vig. (*Delarabrea* Vieill., *Pseudosciadium* Baill. and *Myodocarpus* Brongn. & Gris.) and *Mackinlayeae* R. Vig. (*Apiopetalum* Baill., *Mackinlaya* F. Muell. and several genera of *Hydrocotyloideae* Link (*Apiaceae*)) comprise basally branching lineages within *Apiales*, an interpretation consistent with data from morphology and wood anatomy. Comparison of selected features in these genera, and in close relatives of *Apiales*, suggests that ancestral character states for the order may include: simple leaves, inflorescences in panicles of umbellules, flowers with articulated pedicels and a bicarpellate gynoeceum, an andromonoecious, duodichogamous sexual system, septate fibres, the absence of radial canals, and the presence of paratracheal axial parenchyma in the wood.

*Keywords.* Ancestral characters, *Apiaceae*, *Apiopetalum*, *Araliaceae*, *Delarabrea*, *Mackinlaya*, *Myodocarpus*, phylogeny, *Pseudosciadium*, *Umbelliferae*.

### INTRODUCTION

During the last decade, there has been a remarkable increase in research focusing on various groups within *Apiales*. In large part this has resulted from the application of molecular techniques, which add a powerful new dimension to studies aimed at understanding phylogenetic relationships and delimiting monophyletic groups. At the same time, the number of taxonomists and morphologists studying members of *Apiales* has also been on the rise. Perhaps the most exciting development, however, involves the integration of traditional and more modern approaches, where taxonomic, biogeographic and comparative morphological data are analysed and combined with results from molecular studies. These are evaluated using objective methods in an attempt to untangle the complex and often confounding patterns of character evolution and phylogeny within the order. Ultimately, the use of such largely complementary methods by a broad team of researchers working throughout *Apiales* will enable the development of a phylogenetically based classification system for the order to replace the widely accepted but badly outdated treatments of nineteenth-century authors (e.g. Harms, 1894–97; Drude, 1898).

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Although we are still far from resolving certain complex and troublesome relationships among members of *Apiales* and closely allied groups, a broad consensus is nevertheless developing with regard to the delimitation of several well-defined assemblages that account for the vast majority of genera and species belonging to the order. Specifically, within the last few years a number of molecular studies using both chloroplast and nuclear markers, and focusing on various groups within the order, have consistently supported the recognition of two large 'core' clades. These clades broadly correspond to the traditional definitions of *Apiaceae* (a largely temperate and primarily herbaceous family typically with bicarpellate gynoecia and dry fruits) and *Araliaceae* (mostly tropical trees and shrubs with 5 or more carpels and fleshy fruits) (see Plunkett, 2001 and references therein). These analyses suggest that several additional 'segregate' clades can also be recognized, including two that correspond to the araliad tribes *Myodocarpeae* R. Vig. and *Mackinlayeae* R. Vig. respectively (Plunkett & Lowry, 2001; see also Viguier, 1906, 1925; Lowry, 1986a). Molecular studies further indicate that the apiaceous subfamily *Hydrocotyloideae* Link is polyphyletic, with some members forming basally branching lineages within 'core *Apiaceae*', others belonging within 'core *Araliaceae*', and still others allied to *Mackinlayeae* and perhaps also *Myodocarpeae* (Plunkett, 2001).

Among the groups supported by these recent analyses, several are of particular interest because they exhibit combinations of morphological features that have long prompted botanists to regard them as possible 'intermediates' or 'bridging taxa' between the traditionally defined *Apiaceae* and *Araliaceae* (cf. Rodríguez, 1957, 1971; Philipson, 1970; Thorne, 1973; Judd *et al.*, 1994). These include a number of genera historically placed in *Araliaceae*, but which have various floral and fruit characters that are more typical of *Apiaceae*, such as a bicarpellate gynoecium, petals with an inflexed apex and clawed base, and/or dry, schizocarpic fruits, among others. Confusion regarding the relationships and phylogenetic position of these groups has contributed to difficulties in interpreting trends in character evolution within the order. This in turn has led to problems with assessing the relationships of *Apiales* among the dicots (cf. Plunkett, 2001), and has fueled the erroneous idea that *Araliaceae* represent the 'primitive' end of a sort of phyletic progression culminating in 'advanced' *Apiaceae*. However, with the availability of new data placing these 'intermediates' within distinct, well-differentiated clades in *Apiales*, we have an opportunity to re-examine the apparently anomalous characters they exhibit and to evaluate several new sets of potentially informative features (including those from reproductive biology and wood anatomy). We can then evaluate the possible implications for hypothesizing ancestral character states within the order.

#### BASALLY BRANCHING LINEAGES

##### *The Delarbrea–Pseudosciadium–Myodocarpus group*

Molecular data clearly show that *Delarbrea* Vieill., *Pseudosciadium* Baill. and *Myodocarpus* Brongn. & Gris, which together comprise tribe *Myodocarpeae*, form a

well-defined clade (Fig. 1; see also Plunkett & Lowry, 2001), confirming an earlier interpretation of their monophyly based on morphology and biogeography (Lowry, 1986a,b). These three genera share a number of features, including: a bicarpellate gynoeceum, 5-merous perianth and androecium, articulated pedicels, terminal inflorescences forming panicles of umbellules, clasping petiole bases, imparipinnate leaves (except in the simple-leaved species of *Myodocarpus*), and prominent secretory oil

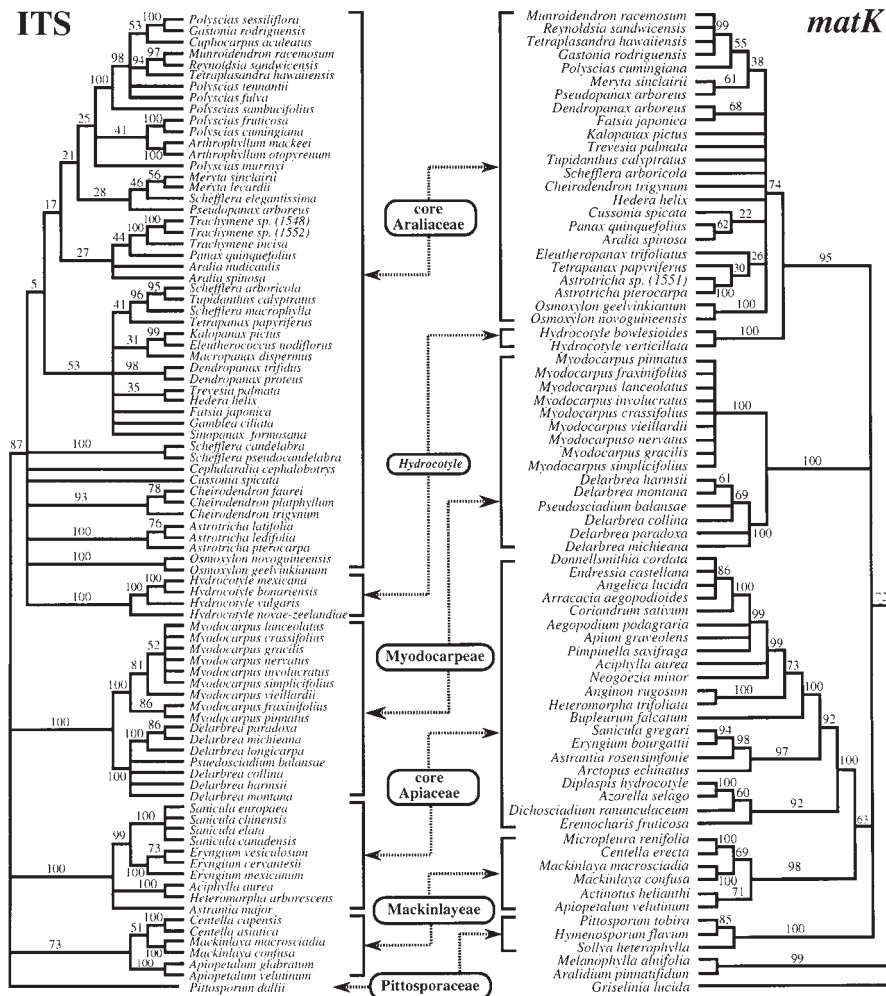


FIG. 1. Strict consensus of 10,000 shortest trees resulting from separate parsimony analyses of ITS (left) and *matK* (right) sequence data, redrawn from Plunkett & Lowry (2001). Bootstrap percentages are provided along the branches, and the major groups of *Apiales* are bracketed and labelled. ITS data set included sequences from 87 taxa; the shortest trees were 1928 steps long with a consistency index (CI, excluding uninformative characters) of 0.392 and a retention index (RI) of 0.734. The *matK* data set comprised sequences from 74 taxa; the shortest trees were 1066 steps long with a CI of 0.567 and a RI of 0.841.

vesicles in their endocarps – the latter character being a synapomorphy for the tribe. Moreover, these genera all exhibit an andromonoecious, duodichogamous sexual system, except for one hermaphroditic species of *Delarbreia* (Schlessman *et al.*, 1990, 2001). They also share several wood anatomical features, including small intervessel pits, homogeneous rays with radial secretory canals, and thick- to very thick-walled libriform fibres, as well as diffuse and diffuse-in-aggregates apotracheal axial parenchyma, which represents another synapomorphy for the group (Oskolski *et al.*, 1997).

*Delarbreia* is centred on New Caledonia, and comprises six species, four of which are endemic to this Pacific island; a fifth species is restricted to Queensland, Australia, and the last member of the genus has one subspecies endemic to New Caledonia and another that extends from there south to Norfolk Island, and to the north and west as far as Timor (Lowry, 1986a). Species of *Delarbreia* are monocaulous to sparsely branched small trees (Figs 2, 3), with flowers whose pedicels are articulated just below the ovary (Fig. 4), drupaceous fruits (Fig. 5) with a fleshy exocarp and a pair of dorsally flattened seeds, free, imbricate petals that are slightly narrowed at the base (but not clawed), and entire, unjointed styles. Among the New Caledonian endemics, two species and one subspecies (*D. paradoxa* Vieill. subsp. *depauperata* Lowry) are restricted to the characteristic serpentine-like ultramafic substrates that cover more than one-third of the island's surface (cf. Lowry, 1998 and references therein), whereas two other species occur exclusively on non-ultramafics; curiously, *D. paradoxa* subsp. *paradoxa* is found only on ultramafics in New Caledonia, but appears to grow on various other substrates elsewhere (Lowry, 1986a).



FIG. 2. *Delarbreia montana* Vieill. ex R. Vig. subsp. *montana*, Dôme de la Tiébaghi, New Caledonia; Lowry 3408 (MO, P).



FIG. 3. *Delarbreia paradoxa* Vieill. subsp. *paradoxa*, Katrikoin, New Caledonia, Lowry *et al.* 4791 (MO, P).



FIG. 4 (left). Flowers of *Delarbreia harmsii* R. Vig., after petals have fallen, Poindimié, New Caledonia, Lowry 3909 (MO, NOU, P).

FIG. 5 (right). Young fruits of *Delarbreia harmsii* R. Vig., Plateau de Dogny, New Caledonia, Lowry 3685 (MO, NOU, P).

The monotypic genus *Pseudosciadium* is endemic to New Caledonia, and appears to occur mostly on ultramafic substrates (Lowry, 1986b). These small, branched trees (Fig. 6) share many features with *Delarbreia*, but differ by having an ovary with a distinct stipe above the pedicel articulation, fruit with a spongy exocarp, and valvate petals that are narrowed to clawed at the base. Although Baillon (1878, 1879) originally suggested that *Pseudosciadium* is closely related to *Myodocarpus*, nearly all subsequent authors placed it in *Mackinlayaeae* (see below) based on the presence of valvate, somewhat clawed petals, an interpretation that has now been refuted by both molecular and non-molecular data (Fig. 1; Oskolski *et al.*, 1997; Plunkett & Lowry, 2001).

*Myodocarpus* is endemic to New Caledonia and comprises ten species of small- to medium-sized trees (Fig. 7), all but two of which are restricted to ultramafic substrates (Lowry, 1986b). Members of this genus are similar to *Delarbreia* and *Pseudosciadium* in habit and certain other features, but can be distinguished by their calyprate (rather than free), imbricate petals, distinctly jointed styles, and dry,



FIG. 6. *Pseudosciadium balansae* Baill., Mt Mou, New Caledonia, *Lowry et al.* 4714 (MO, NOU, P).



FIG. 7. *Myodocarpus lanceolatus* Dub. & R. Vig., La Capture, Plaine des Lacs, New Caledonia, *Lowry et al.* 4692 (MO, NOU, P).

schizocarpic fruits (Fig. 8), which (along with the seeds) exhibit strong lateral compression. The fruits of *Myodocarpus* resemble those of many apioid genera, prompting some authors to regard this genus as a 'link' between *Apiaceae* and *Araliaceae* (e.g. Baumann, 1946; Thorne, 1973). This notion, however, suggests that schizocarps were an ancestral feature in *Apiales*. But as Lowry (1986a,b) indicated, clear homologies can be seen between nearly all fruit structures in *Myodocarpus* and the other members of *Myodocarpeae*, and it is difficult to imagine the evolution of fleshy fruits in *Delarbrea* and *Pseudosciadium*, or in other groups within *Apiales* (e.g. most *Araliaceae*), from dry schizocarps such as those in *Apiaceae* and *Myodocarpus*. It therefore seems more parsimonious to interpret the presence of these fruits in the two groups as a convergence.

Both *matK* and ITS sequence data (Fig. 1; Plunkett & Lowry, 2001) strongly support the hypothesis that the monophyletic group comprising *Delarbrea*, *Pseudosciadium* and *Myodocarpus* occupies a basally branching position within *Apiales*. The molecular data also suggest that *Myodocarpus* is a sister group to a subclade comprising both *Pseudosciadium* and *Delarbrea*. The taxonomic status of *Pseudosciadium*, however, is as yet unsettled: in the ITS tree, this monotypic genus appears to be sister to a monophyletic *Delarbrea*, but trees based on the *matK* data (and a combined data set using both markers; cf. Plunkett & Lowry, 2001) place *Pseudosciadium* within a paraphyletic *Delarbrea*, suggesting that these genera may have to be combined. Additional data are required to clarify these relationships.

The recognition of *Myodocarpus* as a separate subclade within *Myodocarpeae* is supported by the distinctive morphological characters mentioned above, as well as wood anatomical features such as somewhat longer vessel elements, almost exclusively scalariform perforations (vs. simple in the other two genera), thicker-walled fibres, the absence of large bordered fibre pits (present in *Delarbrea* and *Pseudosciadium*), and larger pits on the tangential walls of ray cells (Oskolski *et al.*, 1997). Based on wood anatomical features such as the presence of scalariform vessel-ray pits, two groups can be distinguished within *Myodocarpus*, one comprising the two species with pinnately compound leaves and another group with the eight remaining simple leaved species (Oskolski *et al.*, 1997). Molecular studies also lend some support to this interpretation: the ITS and combined data sets show the



FIG. 8. Fruits of *Myodocarpus fraxinifolius* Brongn. & Gris; Rivière Bleue, New Caledonia, Lowry 3820 (MO, P).

simple-leaved species forming a monophyletic group, although the taxa with pinnately compound leaves either form an unresolved polytomy or a paraphyletic grade at the base of the clade, depending on the analysis (Fig. 1; Plunkett & Lowry, 2001).

#### *The Apiopetalum–Mackinlaya group*

Molecular sequence data indicate a close relationship between *Apiopetalum* Baill. and *Mackinlaya* F. Muell. (Fig. 1; Plunkett & Lowry, 2001), which have traditionally been placed together in the araliad tribe *Mackinlayeae* based on the presence of valvate, clawed petals (cf. Harms, 1894–97; Viguier, 1906, 1925; Hutchinson, 1967). Additional shared characters include sheathing petiole bases, a bicarpellate gynoeceum (2–4 carpels in *Apiopetalum*), inflexed petal apices, and a 5-merous perianth and androeceum (occasionally 6-merous in some *Mackinlaya*) – although each of these features also occurs elsewhere in the order. Both genera are andromonoecious and duodichogamous (Schlessman *et al.*, 1990, 2001; pers. obs.), and they share several notable wood anatomical features, including small intervessel pits, both paratracheal and apotracheal (diffuse and diffuse-in-aggregates in *Apiopetalum* only) axial parenchyma, non-septate fibres, rays composed of mostly upright and square cells, and brown deposits in the vessel elements (Oskolski & Lowry, 2000). Although these wood characters have also been recorded individually elsewhere within *Apiales*, their combined occurrence in *Apiopetalum* and *Mackinlaya* is unique for the order, and supports the suggestion that these genera are closely related.

*Apiopetalum* comprises two species, both endemic to ultramafic substrates on New Caledonia. They are small, well-branched trees with thick, nearly succulent simple leaves, and large, flat-topped compound umbels (Fig. 9). The pedicels are unarticulated, the gynoeceum has 2–4 carpels (Fig. 10), and the fruit is a cylindrical drupe. Distinctive wood anatomical features include small intervessel pits, thick-walled libriform fibres, and especially the presence of diffuse and diffuse-in-aggregates apotracheal axial parenchyma (Oskolski & Lowry, 2000).

*Mackinlaya* has five species, two occurring in tropical Australia (Queensland) and three from the Solomon Islands and New Guinea to Sulawesi and the Philippines (Philipson, 1951, 1979). They are sparsely to well-branched shrubs with palmately compound or simple leaves, and their flowers have articulated pedicels and are arranged in compound umbels of umbellules or cymules. The fruits are fleshy, laterally compressed and strongly bilobed. Several wood characters distinguish *Mackinlaya* from *Apiopetalum*, including narrower and more numerous vessels and rays, and the absence of diffuse-in-aggregates axial parenchyma and of crystals in the ray and parenchyma cells (Oskolski & Lowry, 2000). Some of these differences are probably correlated with habit, especially the very narrow and comparatively numerous vessels and the 1–2-seriate rays in *Mackinlaya*, a trend seen in several other shrubby *Araliaceae*, such as *Oplopanax* (Torr. & A. Gray) Miq. and *Astrotricha* DC.

Both *matK* and ITS sequence data indicate that *Apiopetalum* and *Mackinlaya*





FIG. 9. *Apiopetalum velutinum* Baill., Mt Mou, New Caledonia, Lowry 3309 (MO, P).



FIG. 10. Young fruit of *Apiopetalum velutinum* Baill., Mt Mou, New Caledonia, Lowry 3361 (MO, NOU, P).

comprise a well-supported basally branching clade within *Apiales* (Fig. 1; Plunkett & Lowry, 2001). This group also appears to include several taxa traditionally assigned to *Hydrocotoyloideae* (*Centella* L., *Trachymene* Rudge and *Micropleura* Lag.), supporting earlier studies based on *rbcL* and *matK* data (Plunkett *et al.*, 1996, 1997) and further confirming the polyphyly of the hydrocotoyloids. *Apiopetalum* and *Mackinlaya* share several features with some or all of these genera, including a woody habit (some species of *Centella* and *Trachymene* form woody subshrubs, although all others are herbaceous), simple leaves (lobed to palmate in *Trachymene*), clasping petiole bases (absent in certain *Trachymene*), clawed petals, a bicarpellate gynoecium (2–4 carpels in *Apiopetalum*), and laterally compressed fruits (except in *Apiopetalum*). Again, however, none of these can be regarded as a synapomorphy for the group, as each occurs elsewhere in *Apiales*.

In general, molecular sequence divergence among the woody members of *Apiales* is rather low compared with that of the herbaceous lineage. Between *Apiopetalum* and *Mackinlaya*, however, divergence rates are relatively high, approaching those of the herbaceous apioids (Fig. 1; Plunkett & Lowry, 2001; see also Downie *et al.*, 1998). This may well reflect early divergence between the members of the group,

which would be consistent with the observed morphological and wood anatomical differences.

#### HYPOTHESIZED ANCESTRAL CHARACTER STATES

There is a growing consensus with regard to the composition and relative positions of the basally branching lineages within *Apiales* and the relationships of the order to other members of *Asteridae*. This will soon provide a robust framework against which to evaluate patterns of character evolution and to formulate hypotheses of ancestral character states. Studies conducted thus far appear to be rapidly converging on well-supported circumscriptions of four major lineages within *Apiales* ('core *Araliaceae*', 'core *Apiaceae*', *Myodocarpeae*, and *Mackinlayeae*), but there remain some important differences with regard to the precise branching patterns among these clades (cf. Plunkett & Lowry, 2001). Molecular data also indicate that *Apiales* as a whole are closely related and sister to *Pittosporaceae* (confirming Dahlgren's (1980) earlier interpretation of relationships based on morphology and chemistry), and also to several isolated genera, including *Melanophylla* Baker, *Aralidium* Miq., *Toricellia* DC. and *Griselinia* G. Forst. (e.g. Chase *et al.*, 1993; Plunkett *et al.*, 1996; Soltis *et al.*, 1997). Using this improved understanding of *Apiales* phylogeny, the time seem right to offer some preliminary ideas on possible ancestral characters for the order.

First of all, simple leaves predominate in *Mackinlayeae* and each of the order's apparent close relatives (*Pittosporaceae*, *Melanophylla*, *Aralidium*, *Toricellia*, and *Griselinia*), although in *Myodocarpeae* they occur only in some species of *Myodocarpus*, where they are probably secondarily derived. Within 'core *Araliaceae*', several analyses suggest that the simple-leaved genera *Astrotricha* and *Osmoxylon* Miq. occupy basally branching positions (Plunkett & Lowry, 2001; Wen *et al.*, 2001). Likewise *Hydrocotyle* L., which comprises the sister group to 'core *Araliaceae*' (Plunkett *et al.*, 1996, 1997; Downie *et al.*, 1998, 2001; Plunkett, 2001), has simple leaves.

Most of the genera within the basally branching groups of *Apiales* have panicles of umbellules and flowers with articulated pedicels, the only notable exception being *Apiopetalum*, which has unarticulated pedicels. These same features occur in *Astrotricha*, but the pedicels of *Osmoxylon* lack articulations. The inflorescence structure in *Osmoxylon* is highly specialized (and probably derived), with trifold ultimate branches in which the central axis bears a head or umbellule of sterile, bacciform flowers and the lateral branches have hermaphrodite flowers. Inflorescences of various forms are found among the groups closely related to *Apiales*, but they each have some form of articulation on their pedicels.

Bicarpellate gynoecia are consistently found throughout the basal lineages in *Apiales*, including *Myodocarpeae*, *Mackinlayeae*, *Hydrocotyle* and *Astrotricha*; the only notable exceptions are *Osmoxylon*, which can have from one to many carpels,

and *Apiopetalum* (2–4-carpellate). *Pittosporaceae* are also predominately bicarpellate, as are nearly all members of ‘core *Apiaceae*’. However, carpel number varies among the other related groups, from 1(–2) in *Griselinia*, 2–3 in *Melanophylla*, 3 (with 2 abortive) in *Aralidium*, and 3–4 in *Toricellia*.

An andromonoecious sexual system combined with duodichogamy is almost ubiquitous within *Myodocarpeae* and *Mackinlayeae*, and also appears to occur in most *Astrotricha*. Andromonoecy is also found in many ‘core *Araliaceae*’ and ‘core *Apiaceae*’ (cf. Schlessman *et al.*, 1990, 2001, and references therein), although species of *Osmoxylon* all have protandrous, hermaphrodite flowers. A wide range of sexual systems have been recorded among *Pittosporaceae*, including hermaphroditism, dioecy, gynodioecy, monoecy, and andromonoecy (Cayzer, 1998). Species of *Melanophylla* are hermaphroditic and probably protandrous (Schatz *et al.*, 1998; pers. obs.), whereas dioecy occurs exclusively in *Griselinia* (Philipson, 1967; Dillon & Muñoz-Schick, 1993) and *Aralidium* (Philipson & Stone, 1980), and species of *Toricellia* are dioecious or monoecious (Wangerin, 1910).

With regard to wood anatomy, septate fibres occur in many ‘core *Araliaceae*’, in the woody apioid genera *Heteromorpha* Cham. & Schltdl., *Bupleurum* L., and *Melanoselinum* Hoffm. (Oskolski, 2001), and also in *Pittosporaceae* (Carlquist, 1981), as well as in *Melanophylla*, *Aralidium*, *Toricellia*, and occasionally in *Griselinia* (Noshiro & Baas, 1998). However, they appear to have been lost in both *Myodocarpeae* and *Mackinlayeae*. Similarly, these two tribes are the only groups to have apotracheal rather than paratracheal axial parenchyma, which occurs throughout the rest of the order and among its close relatives, with the exception of *Griselinia*, which has apotracheal (diffuse-in-aggregates) axial parenchyma. Radial canals are found only in *Myodocarpeae*, *Osmoxylon*, and ‘core *Araliaceae*’, plus the woody hydrocotyloid *Trachymene* (Rodríguez, 1957) and the apioid *Steganotaenia* Hoscht.

Based on our current understanding of phylogenetic relations within *Apiales* and the available information for these features, we hypothesize the following ancestral character states for the order as a whole: simple leaves; inflorescences forming panicles of umbellules; flowers with articulated pedicels and most likely a bicarpellate gynoeceium; an andromonoecious, duodichogamous sexual system; septate fibres in the wood; the absence of radial canals; and the presence of paratracheal axial parenchyma. Each of these features is found in some or all of the basally branching lineages within *Apiales* and among many of the order’s closest relatives. While we have not made an attempt to test these hypotheses, it is worth noting that they are highly consistent with the findings reported by Plunkett (2001). It is our hope that presenting these ideas here will help to stimulate future work aimed at evaluating our hypotheses using objective methods in order to improve our understanding of character evolution within the order.

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